RESEARCH ARTICLE

The ontogeny of knuckle-walking and dorsal metacarpal ridge prominence in chimpanzees

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Abstract

Objectives: This study examines the sensitivity of the development of the dorsal metacarpal ridge (DMR) to the frequency of knuckle-walking during ontogeny in chimpanzees, and compares the prevalence and prominence of the DMR in hominoids and baboons.

Materials and Methods: We characterized the type and frequency of quadrupedalism of wild chimpanzees of different ages from the Ngogo community, Uganda. Using museum specimens, we quantified third metacarpal DMR angle and height in *Pan* individuals of different developmental stages, and in adult *Gorilla*, *Pongo*, *Hylobates*, and *Papio*.

Results: When terrestrial, all quadrupedalism consisted of knuckle-walking, although older individuals knuckle-walked more than younger. The total amount of quadrupedalism engaged in by different age groups while arboreal was consistent; however, knuckle usage while arboreally quadrupedal increased with age. The DMR ridge did not emerge in *Pan* until older infancy, after the onset of knuckle-walking, and reached prominence by the juvenile stage. The DMR angle increased significantly after juvenility but relative height did not. Adult *Pan* and *Gorilla* have more prevalent and prominent DMRs than *Papio*; the DMR was rare in *Pongo* and absent in *Hylobates*.

Discussion: The timing of development of the DMR in chimpanzees supports it as a knuckle walking character, as does its occurrence in gorillas, and virtual absence in suspensory *orangutans* and *gibbons*. The DMR in baboons differs in appearance and frequency from DMRs in African apes, and so differentiates knuckle-walking from digitigrady in catarrhines. The relationship between the DMR and loading of a vertical hand while terrestrial deserves further study.

KEYWORDS
digitigrade, *Gorilla*, locomotor development, *Papio*, quadrupedalism

1 | INTRODUCTION

Bipedality is a hallmark of humankind and is frequently used as the sine qua non to recognize our earliest human ancestors (Haile-Selassie, 2001; MacLatchy et al., 2010; Zollikofer et al., 2005). Due to significant gaps in the fossil record, how our ancestors moved before

they became bipedal is unknown, yet multiple hypotheses have been proposed for over a century (Böhme et al., 2019; Fleagle et al., 1981; Keith, 1923; Kimura, 2019; Morton, 1922; Morton, 1924; Prost, 1980; Schultz, 1930; Stern, 1975; Stern & Susman, 1981; Straus, 1949; Tuttle, 1967; Tuttle & Basmajian, 1974; Wood Jones, 1929 to reference a subset see Rose, 1991; Richmond

et al., 2001; Pilbeam & Lieberman, 2017 for reviews). One of the most intensely debated hypotheses is whether early humans evolved from a chimpanzee-like, knuckle-walking ancestor that moved quadrupedally on the ground (Begun, 1992; Dainton & Macho, 1999; Gregory, 1916; Kivell & Schmitt, 2009; Richmond & Strait, 2000; Washburn, 1967; Williams, 2010). Other hypotheses, such as an orangutan-like ancestor that moved upright using orthograde clambering and hand-assisted bipedality in the trees (Crompton et al., 2010; Crompton et al., 2008; Thorpe et al., 2007; Thorpe et al., 2014; see Böhme et al., 2019 for a variant) or a *Proconsul*-like arboreal ancestor that walked on the palms of its hands (Lovejoy & McCollum, 2010; Lovejoy, Suwa, Simpson, et al., 2009; Lovejoy, Suwa, Spurlock, et al., 2009; White et al., 2015) have gained traction recently, but the knuckle-walking hypothesis continues to remain influential (Pilbeam & Lieberman, 2017).

Testing the knuckle-walking hypothesis will depend, in part, on determining if there are skeletal correlates unique to this hand posture, and then looking for these features in the fossil record. Resolving such form-function relationships would be aided by data on the actual hand postures used during locomotion in the wild and further quantification of hypothetically distinctive bony features. Prior studies indicate that knuckle-walking is a rare form of quadrupedalism performed by only two genera of primates, *Pan* and *Gorilla*. During knuckle-walking, the fingers of these apes are tucked under the hand, the metacarpophalangeal (MCP) joints are extended, and the interphalangeal joints are flexed so that the middle phalanges contact the substrate. Additional research shows that quadrupedal walking increases as chimpanzees age (Doran, 1992; Sarringhaus et al., 2014), with infants spending less than a quarter of locomotor time, juveniles spending nearly half, and adolescents and adults devoting the majority of their time moving this way (Sarringhaus et al., 2014). The increase in quadrupedal locomotion from infancy to juvenility is even more pronounced when distance traveled is taken into consideration (Doran, 1992).

Although the approximate timeline of the transition to quadrupedalism has been characterized, the development of knuckle-walking per se has yet to be determined. Adult chimpanzees primarily knuckle-walk when moving quadrupedally, but prior studies indicate that knuckle-walking develops gradually (Doran, 1992; Kimura, 1986; Sarringhaus, 2013). Doran (1992) observed one infant chimpanzee (4–6 months) using its palms during a bout of quadrupedal locomotion. Doran (1992) documented older infants (6 months to 2 years) knuckle-walking in 2 of 8 quadrupedal bouts. Additional qualitative observations suggested to Doran that the degree to which chimpanzees knuckle-walk during ontogeny depends in part on whether they are arboreal or terrestrial (Doran, 1992). These observations provide a valuable framework for tracking the development of knuckle-walking, but small samples and the lack of quantitative data on the behavior preclude making any general conclusions.

Given the hypothesis that the evolution of bipedalism involved a knuckle-walking phase, there has been considerable scrutiny of possible anatomical correlates of knuckle-walking hand postures. The wrist has been a region of interest in this regard, and several anatomical features have been proposed to be related to knuckle-walking behavior, including articular facets in the capitate (Corruccini, 1978; Wuthrich et al., 2019), distal projection of the dorsal radius (Richmond et al., 2001; Tuttle, 1967), and os central fusion (Kivell & Begun, 2007; Orr, 2018). However, no single wrist feature has emerged as unequivocally predictive of knuckle-walking behavior, as some features such as os central fusion and distal radial projection are not unique to knuckle-walking apes (see Kivell, 2016 for a review). Moreover, some features of the wrist, such as degree of capitate waisting, manifest along a continuum among genera (Kivell & Schmitt, 2009). A recent multivariate study successfully partitioned *Pan* and *Gorilla* from Asian apes and other catarrhines using anatomical landmarks associated with capitate surface architecture (Wuthrich et al., 2019). However, this study also noted that individual knuckle-walking traits are not exclusively associated with knuckle-walking, and that inferring this positional behavior from wrist morphology remains challenging.

The metacarpal (MC) represents another promising bone for detecting anatomical signatures of knuckle-walking, as the hyperextension that occurs at the metacarpal phalangeal (MCP) joint during hand contact with the substrate is predicted to direct loads to the dorsal aspect of the MC head (Chirchir et al., 2017; Zeininger et al., 2011). In contrast, suspension and climbing are predicted to preferentially load the distal and palmar aspects of the MC heads, respectively (Chirchir et al., 2017; Zeininger et al., 2011). Some support for this prediction comes from studies of the internal trabecular distribution in the third MC head of chimpanzees and other hominoids. Although imaging, sampling and analytical methods have varied, multiple studies have found that trabecular bone in the dorsal aspect of the metacarpal head has a relatively high bone volume fraction in knuckle-walkers compared to other hominoids (Chirchir et al., 2017; Dunmore et al., 2019; Tsegai et al., 2013). In contrast, Barak et al. (2017) did not find a relatively high bone volume fraction in the dorsal metacarpal head of chimpanzees, but did detect an architectural difference between humans and chimpanzees, with the 3D principal trabecular orientation aligning with the long axis of the metacarpal shaft in humans, but deviating either medially or laterally in chimpanzees. The authors argued this orientation possibly reflects directional loading on the MC head that results from subtle responses by the hands in balancing more lateral or medial hindlimb postures. Matarazzo (2015) also found that trabecular alignment in the metacarpal head of knuckle-walkers is distinguishable from that of suspensors and generalized quadrupeds, while Zeininger et al. (2011) has demonstrated lower mineralization in the dorsal aspect of the third MC head of chimpanzees compared to humans, possibly reflecting higher rates of bone remodeling in this region due to the joint reaction forces generated by knuckle-walking.

The dorsal aspect of the MC head has also been shown to have a dorsal metacarpal ridge (DMR). This raised ridge of bone on the distal end of the MC has been hypothesized to be a knuckle-walking feature that acts to stabilize the metacarpophalangeal joint during hyperextension (Lewis, 1977; Sarmiento, 1994; Tuttle, 1967; Williams, 2010). Furthermore, the DMR is purportedly found in knuckle-walking gorillas and chimpanzees but is absent in non-knuckle-walking

humans, gibbons, and orangutans (Lewis, 1977; Preuschoft, 1973; Richmond et al., 2001; Susman, 1979; Tuttle, 1967). The DMR is present most often on the third MC in African apes (79%–100%) and displays variation in its incidence and degree on other digits (Inouye, 1994; Inouye & Shea, 2004; Susman, 1979). The third MC is also the digit loaded most consistently by captive chimpanzees, while there is less variation in gorilla loading patterns (Matarazzo, 2008; Wunderlich & Jungers, 2009). Adult *Pan troglodytes*, *Gorilla gorilla*, and *Gorilla beringei* display the DMR more frequently than do subadults, and the height of the feature scales with body size (Inouye & Shea, 2004). Taken together, the preceding observations suggest that the DMR is a plastic feature that forms during ontogeny, a period when bones are most sensitive to repeated locomotor activity (Lieberman et al., 2003; Pontzer et al., 2006; Turner et al., 1995).[1] Nonetheless, the precise time the DMR starts to emerge during development in the African apes remains unclear.

The DMR has anecdotally been noted to be present in large-bodied digitigrade primates such as *Papio* (Richmond et al., 2001), a taxon that aligns the manus vertically with hyperextended metacarpophalangeal joints (Patel, 2010). During digitigrade locomotion, the MC head is load bearing and projected to experience the greatest strain on the dorsal and central sides (Chirchir et al., 2017). The presence of the DMR in African apes and baboons suggests that the DMR may not represent a unique knuckle-walking feature. Instead, the DMR may be a MCP joint stabilizer during MCP hyperextension for individuals above a certain body size that engage in habitual terrestriality, whether through digitigrady or knuckle-walking (Orr, 2005; Patel & Maiolino, 2016; Richmond et al., 2001). Testing this hypothesis requires comparing DMR prevalence and prominence in digitigrade *Papio* and knuckle-walking *Pan* and *Gorilla*.

While multiple researchers have attributed a stabilizing, functional role to the DMR during knuckle-walking and/or digitigrady (Lewis, 1977; Orr, 2005; Patel & Maiolino, 2016; Richmond et al., 2001; Sarmiento, 1994; Tuttle, 1967; Williams, 2010), Simpson et al. (2018) have challenged this interpretation on two grounds. First, they suggest that the ridge cannot act as a stabilizer because regular loading of the adult bone in this fashion would lead to osteoarthritis, and second, they suggest that the DMR is an incidental byproduct of loads experienced by the subadult cartilaginous epiphysis during knuckle-walking. This caution is warranted. However, addressing whether the DMR is a direct stabilizer or a byproduct of habitual use would require clinical and/or experimental approaches beyond the scope of this study.

There are three goals of this study. First, we assess the onset of knuckle-walking in chimpanzees, a behavior characterized by alterations in the hand- and wrist-loading environment. We document developmental changes in the loading environment by differentiating hand contact and degree of arboreality used by chimpanzees of different ages. We then test the hypothesis that hand posture changes during ontogeny, with knuckle-walking increasing with increasing quadrupedalism and terrestriality. Our second goal is to assess changes in chimpanzee DMR features over the same developmental timeline through an analysis of an ontogenetic series of aged MCs

from museum collections. Here we investigate whether the DMR changes during development in tandem with the change in loading environment experienced by the wrist and hand with the onset of knuckle-walking. Specifically, we seek to determine whether DMR development tracks knuckle-walking. Such tracking would be consistent with a phenotypic plasticity explanation, although it does not unequivocally demonstrate it. Third, we attempt to ascertain whether DMR morphology is unique to knuckle-walkers. To do so, we conduct comparisons between chimpanzees and other primate species, who move in different ways, and test three hypotheses:

The null hypothesis (H0) proposes that the DMR is not affected by hand usage. H0 predicts that the presence and prominence of the DMR will fail to track the development of knuckle-walking in chimpanzees (i.e., it will not increase with increasing knuckle usage). It also predicts that the prevalence and prominence of the DMR will not vary among genera (*Pan*, *Gorilla*, *Papio*, *Pongo*, and *Hylobates*) according to hand usage.

The first alternate hypothesis (H1) proposes the DMR reflects knuckle-walking. This hypothesis predicts that the DMR will develop after subadult *Pan* start to knuckle-walk and that the DMR will be more prevalent and prominent in *Pan* and *Gorilla* compared to *Papio*, *Pongo*, and *Hylobates*.

The second alternate hypothesis (H2) proposes that the DMR reflects vertical manus terrestrial quadrupedalism, including both knuckle-walking and digitigrady. Like H1, H2 predicts that the DMR will develop after knuckle-walking in subadult *Pan*. Additional predictions of H2 are that the DMR will be prevalent in adult *Pan*, *Papio*, and *Gorilla* but not in *Pongo* and *Hylobates*, and furthermore, that the prevalence and prominence of the DMR will be similar among *Pan*, *Gorilla*, and *Papio*.

2 | MATERIALS AND METHODS

2.1 | Behavioral methods

Data on the locomotor behavior of chimpanzees were collected by L.S. at Ngogo, Kibale National Park, Uganda. The unusually large size of the Ngogo community (approximately 160 individuals) provided a rare opportunity to sample the locomotor behavior of many chimpanzees who varied in age. Chimpanzees were divided into four age categories: infants (0.1–5 years), juveniles (5.1–10 years), adolescents (10.1–15 years), and adults (15+ years; Table 1). When examining only infants, the largest increase in quadrupedal locomotion occurs when individuals reach 3 years of age (Sarringhaus et al., 2014; Table 1). The infant category therefore was further divided into *young infant* (≤3 years) and *old infant* (3–5 years) groups. Ages of subadults were determined based on their birth dates known to within a few days or a calendar year (Wood et al., 2017). The birth dates of some adults were estimated, as these individuals were all over 20 years of age. Their ages were assigned using genealogical information, derived from genetic data and behavioral observations, and information regarding their physical appearance (Wood et al., 2017). Sarringhaus

TABLE 1 Morphological and behavioral markers of chimpanzee age categories

Category	Age[a]	Locomotor behavior[b]	Dental eruption markers[c]
Young Infant	0–3	Predominantly suspensory with the highest levels of suspensory behavior for any age group.	deciduous dentition
			M1 not erupted
Old Infant	3.1–5	Still predominantly suspensory but higher levels of independence from mother and higher levels of quadrupedal locomotion compared to young infants.	M1 erupts
			I1 and M2 not erupted
Juvenile	5.1–10	Completely independent from mother, a substantial decrease in suspensory locomotion and increase in quadrupedal walking and running compared to older infants.	I1 & M2 erupted,
			C frequently erupts at this time
			M3 not erupted
Adolescent	10.1–15	A substantial decrease in suspensory locomotion and vertical climb and increase in quadrupedal walking compared to juveniles.	C fully erupted
			M3 erupts at this time
			postcrania not all fused
Adult	15+	No significant change in locomotion compared to adolescents.	Some wear on teeth, postcrania all fused[d]

[a]Absolute ages used for behavioral research.
[b]Sarringhaus et al., 2014; Doran, 1992.
[c]Dental age markers used to create age categories for anatomical specimens. Dental markers were used to classify museum specimens according to age, as they correspond to chronological and behavioral age categories (Machanda et al., 2015; Smith et al., 1994; Smith et al., 2010; Smith et al., 2013; Smith & Boesch, 2011).
[d]Postcrania from Zihlman et al., 2007.

et al. (2014) provides additional details and a rationale for how age groups were defined.

Rates of arboreal and terrestrial quadrupedal locomotion were calculated using observations of 53 chimpanzees, including 9 young infants, 11 old infants, 11 juveniles, 11 adolescents, and 11 adults. Each of these chimpanzees was sampled during five observation sessions, each of which was 1 h long. During observation sessions, the positional behavior of focal individuals was recorded every 2 min during instantaneous scan samples. Chimpanzee positional behavior was classified according to body parts that bear the individual's weight, using categories defined in prior studies (Hunt et al., 1996; Sarringhaus et al., 2014; Thorpe & Crompton, 2006). Quadrupedal locomotion included both quadrupedal walking and running. The percentage of time members of each age class spent in quadrupedal locomotion was calculated for arboreal and terrestrial substrates. Rates of arboreal and terrestrial quadrupedal locomotion were normally distributed and analyzed using analysis of variance (ANOVA) with Tamhan T's posthoc comparisons as equal variance was not assumed (Sarringhaus et al., 2014).

The hand placements of chimpanzees during quadrupedal locomotion were recorded and included three categories: knuckle, palmigrade grasp, and palmigrade non-grasp. In knuckle, the intermediate phalanges on digits II–V contact the substrate. In palmigrade grasp, the palm and at least two digits are in contact with

the substrate, and the digits are used to grasp the substrate. In palmigrade non-grasp, the palm contacts the substrate but the fingers do not grasp the substrate. Quadrupedal locomotion was also coded as occurring on terrestrial or arboreal substrates. The preceding data were collected over 340 h observing chimpanzees with hand contact recorded in 789 of the 960 instances of quadrupedal locomotion (Sarringhaus et al., 2014). Because quadrupedal locomotion occurs infrequently in infants, especially young infants, 32 h of locomotor video footage were also analyzed to determine hand usage during quadrupedal locomotion. Videos were recorded by LS on two cameras, a Canon 2GL and a Canon XHAI HDV 3CCD, and analyzed frame-by-frame. For each locomotor bout, the hand postures of individuals were recorded from the second visible forearm step. Video data were recorded in the same manner as in focal observations, resulting in 563 samples of chimpanzees moving quadrupedally. There was no overlap in data derived from video bouts and focal observation sessions. Hand contact data were derived from 119 individuals, including 10 young infants, 11 old infants, 16 juveniles, 21 adolescents, and 61 adults.

Hand contact data during arboreal locomotion were analyzed using a negative binomial regression with data aggregated by individual ID (Hilbe, 2011; SPSS v.26). Terrestrial quadrupedal walking and usage was too homogenous to include in the model (see results). The dependent variable was the number of times individuals used their

knuckles while moving. The predictor variable was age coded as a continuous variable in years. We included the natural log of the number of times individuals engaged in arboreal quadrupedal walking as an offset in the model.

2.2 | Skeletal methods

The MCs of 323 wild-caught individual primates from seven museums were assessed (see Table 2). The 173 chimpanzee skeletal specimens were partitioned into age categories based on tooth eruption (see Table 1, Smith et al., 1994; Smith et al., 2010; Smith & Boesch, 2011, Smith et al., 2013; Machanda et al., 2015). Specifically, we used maxilla tooth alveolar eruption to separate individuals into age categories of young infant (no first molar [M1] erupted), old infant (M1 but no second molar [M2] erupted), juvenile (M2 but no canine [C] erupted), and adolescent (C erupted but epiphyses not fused, Table 1). Adults had C and third molar (M3) erupted and all postcranial epiphyseal sutures fused. These tooth eruption patterns were translated into age estimates in years (see Table 1) so that the timing of the onset of skeletal features can be directly compared to the timing of the behavioral transitions we document among individuals of known age in our locomotor study.

The MCs of *Gorilla*, *Papio*, *Hylobates*, and *Pongo* were also analyzed to incorporate comparisons to species who moved in similar and different ways from chimpanzees (Table 2). The third MC was chosen for examination because the third ray has been reported to be used consistently during knuckle-walking by captive African apes while the use of the other digits is more variable (Inouye, 1994). Even when digits II–V are used during knuckle-walking, the third middle phalanx consistently bears the greatest weight in captive chimpanzees (Matarazzo, 2008; Wunderlich & Jungers, 2009), suggesting that MC III will display morphological changes related to the inception of knuckle-walking, if such changes exist.

The DMR was measured using ImageJ software from photographs of the bone taken in medial view. MCs were aligned (using clay) so that the ventral and dorsal anterior–posterior diaphyseal surface midpoints, just proximal to the metaphysis, were equidistant from the supporting surface. The distal and proximal surfaces were in anatomical position. Measurements were standardized using a 1 cm scale, positioned in the same plane as the bone, in each image. The presence and degree of the DMR was assessed using Inouye's MC torus measurement method (Inouye, 1994; Inouye & Shea, 2004), which involves measuring the ridge angle (formed by drawing lines between the three points labeled A, B, and C, Figure 1) and ridge height (the distance from point C perpendicular to the 180° line (Figure 1)). If the angle formed by ABC

TABLE 2 Dorsal metacarpal ridge angle and height for different age classes and genera of primates

| Category | DMR angle (all individuals) | | DMR angle <180 (only DMR present) | | DMR height in mm (all individuals) | | DMR height <180 (only DMR present) | |
	N	Mean (SD)	N	Subset mean (SD)	N	Mean (SD)	N	Mean (SD)
Pan adult	45	158.91 (8.46)	44/45	158.43 (7.91)	45	1.47[d] (0.87)	44	1.50 (0.85)
Pan subadult	125[a]	171.30 (10.14)	75/125	165.27 (9.18)	125	0.58 (0.71)	74	0.96 (0.65)
Young Inf.[b] (Pre M1)	17	180 (0)	0/17	NA	17	0	0	NA
Old Inf. (M1 pre M2)	51	176.09 (6.30)	21/51	170.50 (6.61)	49	0.24 (0.44)	21	0.59 (0.51)
Juvenile (M2 pre C)	30	167.04 (8.33)	28/30	166.10 (7.82)	31	0.93 (0.70)	28	0.99 (0.67)
Adolescent (C)	25	160.02 (10.04)	25/25	160.02 (10.05)	25	1.29 (0.65)	25	1.29 (0.65)
Gorilla adult	29	151.63 (11.76)	28/29	150.62 (10.62)	29	2.55[e] (1.35)	28	2.64 (1.28)
Gorilla subadult	44	170.27 (9.62)	28/43	164.71 (7.70)	44	0.77 (0.87)	28	1.20 (0.80)
Pre M1	5	180.00 (0)	0/5	NA	5	0	0	NA
M1 pre M2	17	174.65 (7.18)	8/17	168.64 (6.30)	17	0.36 (0.48)	8	0.77 (0.42)
M2 pre C	17	167.96 (6.60)	15/17	166.36 (5.13)	17	0.93 (0.60)	15	1.06 (0.52)
C not fused	4	151.66 (5.56)	4/4	151.66 (5.56)	4	2.61 (0.96)	4	2.61 (0.96)
Pongo adult	16	178.38 (3.56)	3/16	171.37 (2.02)	16	0.04 (0.11)	3	0.22 (0.17)
Hylobates adult	41	180 (0)	0/41	NA	41	0.00	NA	0
Papio adult[c]	20	174.11 (7.30)	11/20	169.29 (6.68)	20	0.17 (0.24)	11	0.31 (0.24)

Note: Primate specimens were from the American Museum of Natural History, Cleveland Museum of Natural History, Harvard Museum of Comparative Zoology, Natural History Museum London, Naturkundemuseum Stuttgart, the University of Zurich, and the Quex Museum (Kent, U.K.).
[a]Two chimpanzee subadult individuals are subadult but have no reliable age estimates.
[b]Inf = infant.
[c]Nine baboon individuals were measured from the lateral side. No difference between samples measured from the lateral and medial side for baboons $F = 0.864$, $df = 1,21$, $p = 0.363$).
[d]Compared to Inouye height measurement of *Pan troglodytes* for 1.42 (0.96).
[e]Compared to Inouye *Gorilla beringei* 1.84 (1.53) and *Gorilla gorilla* 2.41 (1.77).

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was approximately a straight line (180° or greater), a DMR was considered absent. If the ridge angle was less than 180°, a DMR was considered present. All angle measurements were capped at 180°; while this method detects a dorsal ridge, it is not ideal for assessing the extent of roundedness of the MC head, however, we are not assessing this condition in this study. The DMR angle was used for comparative analysis because it captures ridge prominence in specimens more precisely than simply recording presence or absence of the trait using the 180° threshold. Angle was used as it is a dimensionless unit and even the absence of a ridge produces a numeric value. Angle degrees were converted to radians (1 rad $= 180/\pi$) for analysis.

Inouye has demonstrated that MC length does not scale with body size in *Gorilla* and *Pan* (1992 & 1994). Long bone midshaft diaphyseal measurements and joint dimensions are generally better at inferring body size than lengths (Burgess et al., 2018; Ruff, 2002). Therefore, we measured metacarpal midshaft anterior–posterior diameter from the medial-view photographs as a proxy for body size. We performed a linear regression for LN (ridge height) on LN (AP diameter) and found $R^2 = 0.225$ and $R^2 = 0.286$ for chimpanzees and gorillas respectively. As ridge height data were not normally distributed (at least one group test $p < 0.05$), the regression p values cannot be used to assess significance of the relationship between ridge height and AP diameter. Previous work has shown that ridge height scales with body size (Inouye & Shea, 2004). We therefore use the natural log of the ratio of ridge height/AP diameter in analyses to account for body size differences when making comparisons among individuals in the same and different genera (see Jungers et al., 1995 for the merits of using ratios).

Because the data were not normally distributed, we used nonparametric statistics in all of the analyses. We used Kruskal-Wallis tests to examine heterogeneity among multiple groups, and conducted pairwise posthoc comparisons with Bonferroni corrections to determine whether differences existed between specific groups (Sokal & Rohlf, 1995). In these analyses, individuals were categorized into the five age groups corresponding to dental eruption categories described above. We analyzed angle differences using all individuals.
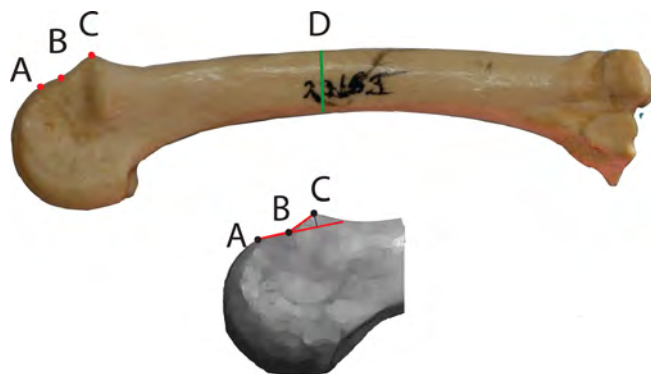
Our analyses of height differences included only those individuals who displayed a ridge. We used Mann–Whitney U tests to compare sex differences in the DMR heights and angles of adult chimpanzees and gorillas (Siegel & Castellen, 1988).

3 | RESULTS

3.1 | Locomotor development in chimpanzees

As chimpanzees developed, they spent an increasing amount of time moving quadrupedally, and also shifted to proportionally more terrestrial as opposed to arboreal quadrupedalism (Figure 2). Young and old infants spent only a small percentage of their time moving quadrupedally (11% and 24% of locomotor behavior respectively, Figure 2), but the latter did so significantly more than the former (Mann–Whitney $p = 0.046$; see Sarringhaus et al., 2014). When moving quadrupedally, both young and old infants did so more often in the trees than the ground (Figure 2). In contrast, quadrupedalism was primarily a terrestrial activity for juveniles, adolescents, and adults (Figure 2). Individuals in different age groups did not vary in the amount of locomotor time spent moving quadrupedally in the trees (ANOVA $F = 1.510$, $p = 0.213$; Figure 2). The amount of locomotor time spent moving quadrupedally on the ground, however, displayed heterogeneity among the five different age classes (ANOVA $F = 35.887$, $p < 0.001$; Figure 2). Pairwise posthoc tests revealed that members of older groups engaged in more terrestrial quadrupedalism than individuals in younger groups ($p < 0.05$ for all comparisons), except old versus young infants and adolescents versus adults ($p = 0.926$ and 0.878, respectively; Figure 2).

We examined the way chimpanzees used their hands during terrestrial and arboreal quadrupedalism. During 1008 instances of terrestrial quadrupedal locomotion, chimpanzees of all ages engaged in knuckle-walking 100% of the time (Figure 3). By contrast, chimpanzee
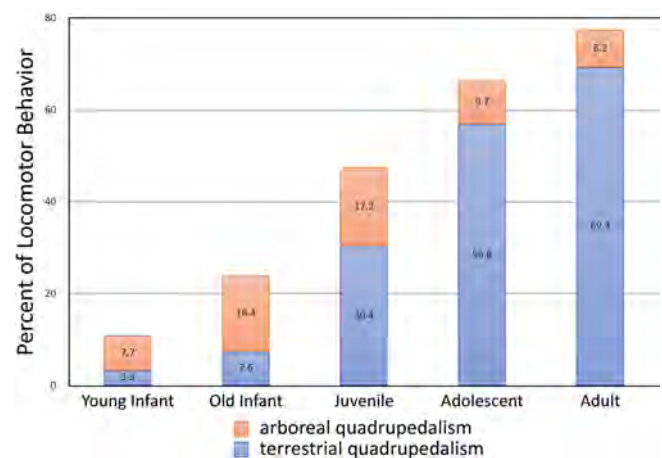

FIGURE 1 Measurement of the dorsal metacarpal ridge. Angle <ABC (measured in radians) is used to quantify the presence of the DMR. DMR height is measured as the length of the line perpendicular to the 180 degree line connecting points A and B, that intersects with point C. Line D represents the midshaft diameter

FIGURE 2 Quadrupedal locomotion by chimpanzees in different age classes. The proportion of time spent moving quadrupedally arboreally (orange) and terrestrially (blue) is shown relative to all locomotor behavior
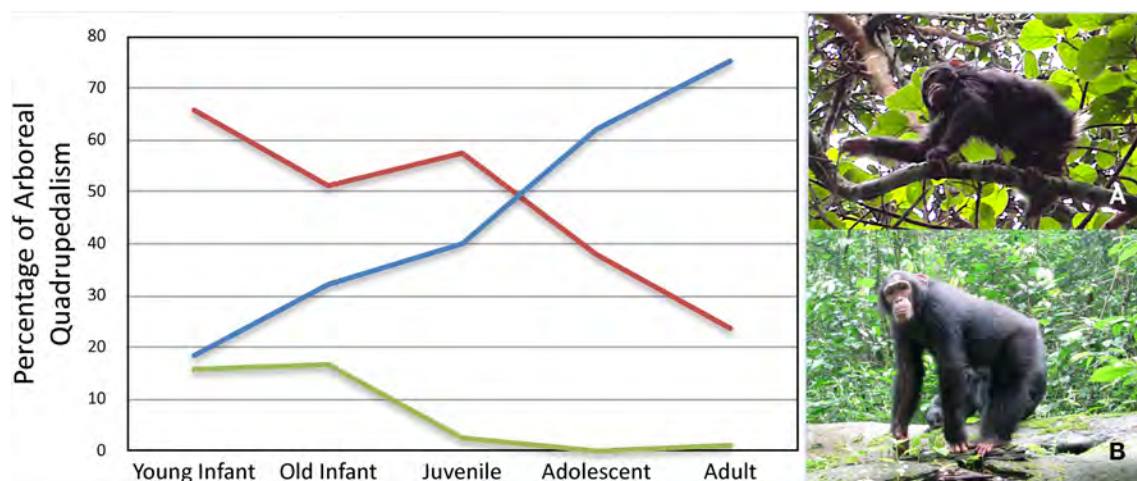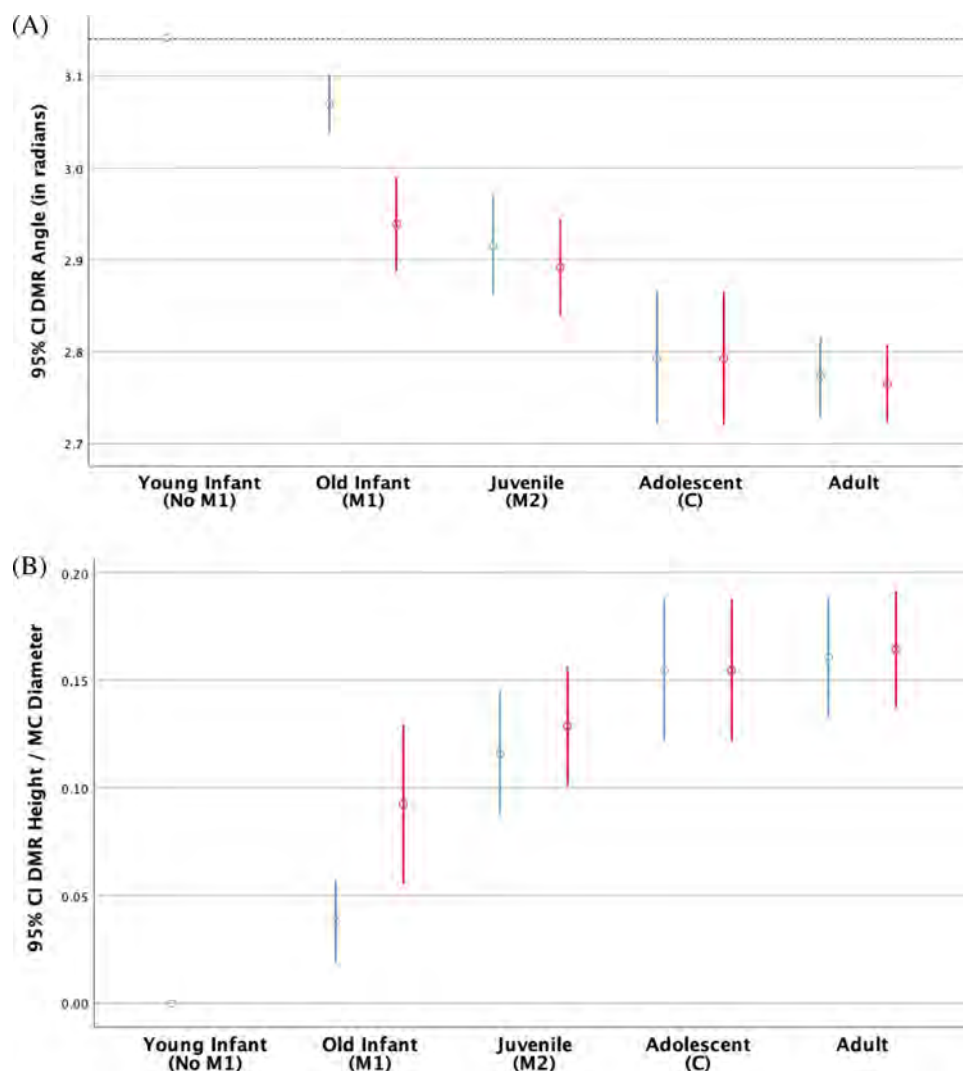
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FIGURE 3 Hand contact during arboreal quadrupedal locomotion. Red line = palm grasp, green = palm non-grasp, blue = knuckle. Results show combined video and frequency data. Image (a) is an example of palmigrade grasp hand posture. image (b) is an example of knuckle hand posture

FIGURE 4 (a) Distal metacarpal ridge angles (in radians) in chimpanzees of different age classes. Means and 95% confidence intervals are shown. The dashed line at 3.14 radians indicates that the epiphyseal area is straight or rounded with no distal metacarpal ridge present. Below 3.14 indicates a distal metacarpal ridge is present. (b) Chimpanzee distal metacarpal ridge height/MC diameter in chimpanzees of different age classes. Means and 95% confidence intervals are shown. Blue data are all individuals. Red data are only individuals with the feature present. Blue data young infant $N = 17$, old infant $N = 51$, juvenile $N = 30$, adolescent $N = 25$, adult $N = 45$; red data old infant $N = 21$, juvenile $N = 28$, adolescent $N = 25$, adult $N = 44$

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hand use during arboreal quadrupedalism varied as chimpanzees aged, with individuals employing three distinct types of hand positions: knuckle, palm grasp, and palm non-grasp (Figure 3). Individuals in both young and old infant groups employed all three of these hand postures but predominantly used palm grasp when moving arboreally (Figure 3). As chimpanzees grew older, their hand use during arboreal quadrupedalism changed. For every one-year increase in age, knuckle-usage increased by 33% (Exp[B] = 1.033, CI = 2.3%–4.4%, $p < 0.001$). Including age as a predictor in a negative binomial regression analysis improved the fit of the model compared to the null model that excluded predictors ($X^2[1] = 8.135$, $p < 0.004$).

3.2 | Dorsal metacarpal ridge

3.2.1 | Dorsal metacarpal ridge development in chimpanzees

The DMR was present to variable degrees in chimpanzees of different ages. The DMR was absent in all young infants with no M1 but had developed (angle <180°) in 41% of the old infants, whose M1s had erupted (Table 2, Figure 4). The DMR was present in 93% of the juveniles, defined as individuals whose M2s had erupted, and in 98%–100% of the adults and adolescents (Table 2, Figure 4). In individuals with a ridge present, LN (DMR height) and angle (radians) were inversely correlated; those with large DMR heights possessed small angles ($r_s = -0.837$, $p < 0.05$).

The DMR angle varied among chimpanzees in the different age classes (Kruskal-Wallis $H = 97.041$, $p < 0.001$; Figure 4a). Pairwise post-hoc tests revealed that the DMR became more prominent as chimpanzees aged, that is, the DMR angle decreased with age. Young and old infants possessed DMRs with relatively larger angles. They did not differ from each other ($p = 0.755$), but their DMR angles were much larger than those of members in all other age groups ($p < 0.001$ for all comparisons). The DMR angle continued to remain relatively large during juvenility but differed from the smaller angle in adults ($p < 0.001$). Finally, the DMR angle by adolescence converged on those found in adults, as the values did not differ significantly ($p = 1.00$, Figure 4a blue lines).

DMR height varied among chimpanzees of different ages (Kruskal-Wallis H 12.10, $p = 0.007$; Figure 4b). While mean height increased as chimpanzees aged (Table 2 & Figure 4b), pairwise post-hoc tests indicated that only old infants differed from adults in this
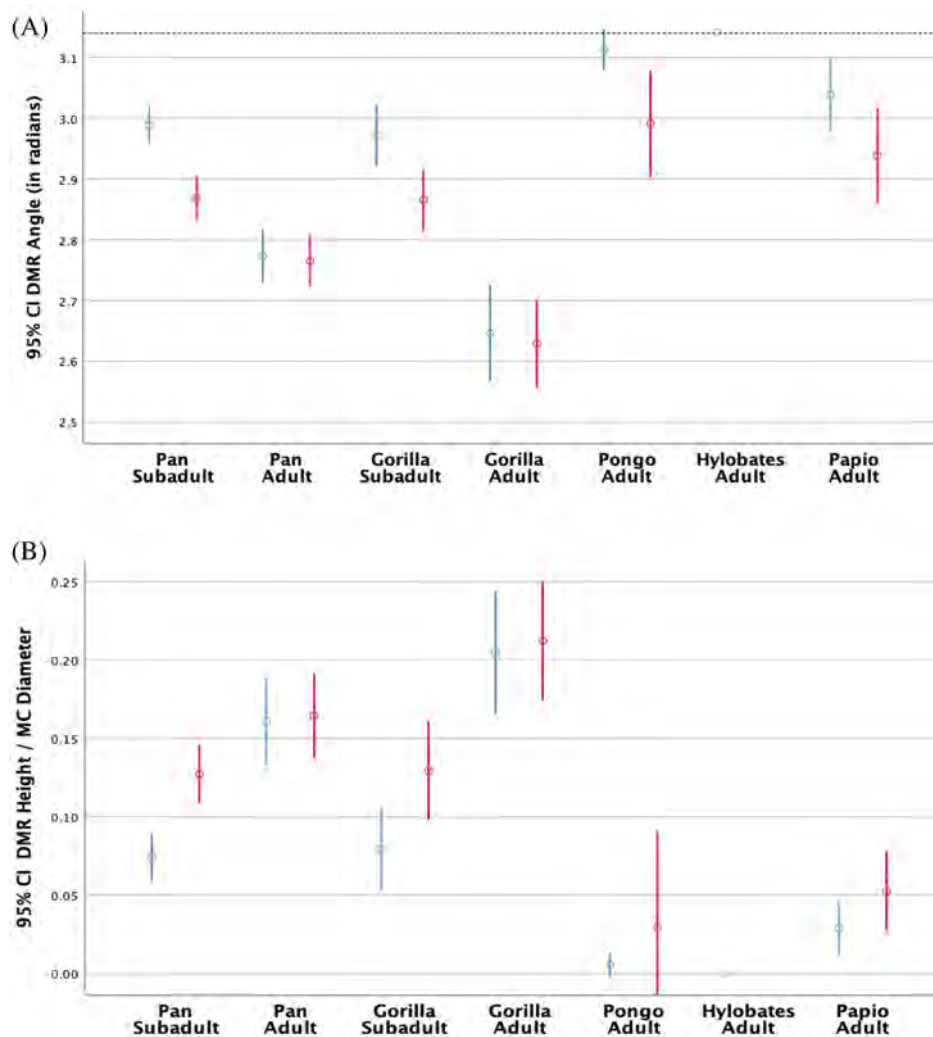

FIGURE 5 (a) Distal metacarpal ridge angles (in radians) in *Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Papio*. Means and 95% confidence intervals are shown. The dashed line at 3.14 radians indicates that the epiphyseal area is straight or rounded with no distal metacarpal ridge present. Below 3.14 indicates a distal metacarpal ridge is present. (b) Distal metacarpal ridge height/MC diameter in *Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Papio*. Means and 95% confidence intervals are shown. Blue data are all individuals. Red data are only individuals with the feature present. Blue data *Pan* subadult $N = 125$, *Pan* adult $N = 45$, *Gorilla* subadult $N = 43$, *Gorilla* adult $N = 29$, *Pongo* adult $N = 16$, *Hylobates* adult $N = 41$, *Papio* adult $N = 20$. Red data *Pan* subadult $N = 75$, *Pan* adult $N = 44$, *Gorilla* subadult $N = 28$, *Gorilla* adult $N = 28$, *Pongo* adult $N = 3$, *Papio* adult $N = 11$

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TABLE 3 Kruskal-Wallis post hoc results for DMR angle (green) and height (purple)

	Pan SA	Pan	Gorilla SA	Gorilla	Pongo	Hylobates	Papio
Pan SA	X	0.536	1.000	*0.001*	NA	*NA*	*0.049*
Pan	*<0.001*	X	1.000	0.792	NA	NA	*0.001*
Gorilla SA	1.000	*<0.001*	X	*0.020*	NA	NA	0.115
Gorilla	*<0.001*	1.000	*<0.001*	X	NA	NA	*<0.001*
Pongo	0.118	*<0.001*	0.104	*<0.001*	X	NA	NA
Hylobates	*<0.001*	*<0.001*	*<0.001*	*<0.001*	1.000	X	NA
Papio	1.000	*<0.001*	1.000	*<0.001*	1.000	0.148	X

Note: Pairwise comparison results shown with Bonferroni correction for multiple tests. SA indicates subadults, all other groups comprised of adult specimens. Angle (using radians) for ALL individuals were compared and height was compared ONLY between individuals with ridge PRESENT using LN DMR height/MC midshaft AP diameter (as LN transformation produces no value for ratios equivalent to zero). Bold values are significant p < 0.05.

regard ($p = 0.011$, all other comparisons $p > 0.05$). Ridge height cannot be analyzed for young infants because these individuals lacked ridges Figure 4b).

3.2.2 | Dorsal metacarpal ridge comparisons among genera

While almost all adult *Pan* (98%; $n = 43/44$) and *Gorilla* (97%; $n = 28/29$) MCs possessed ridges, they were rare or absent in other taxa. None of the *Hylobates* specimens displayed ridges ($n = 41$); however, ridges were present in a few *Pongo* individuals ($n = 3/16$) and about half of the *Papio* ($n = 11/20$) specimens. The presence of the ridge does not seem to be a function of size. The *Pongo* and *Papio* individuals with a ridge present were not those with the largest MC midshaft AP diameter. For example the *Pongo* individual with largest DMR had a MC diameter = 6.714 mm, below the *Pongo* mean of 8.93 mm, but not the smallest individual (range = 6.1–14.25 mm). Moreover, lack of a ridge in *Gorilla* and *Pan* did not occur in the smallest individuals (as measured by diameter). For example, the one *Gorilla* adult who lacked a DMR had an MC diameter = 11.8 mm, just below the *Gorilla* adult mean of 12.40 mm (range = 9.47–15.15 mm). The one *Pan* adult who lacked a ridge had a MC diameter = 8.95 mm, close to the adult mean of 9.03 mm (range = 7.3–11.2 mm).

The angle of the DMR varied among subadult and adult *Pan*, subadult and adult *Gorilla*, adult *Pongo*, adult *Hylobates*, and adult *Papio* (Kruskal-Wallis *H* 144.181, *df* = 6, *p* < 0.001, Figure 5a). Post hoc tests indicated that the DMR angles of adult *Pan* and *Gorilla* did not differ from one another, but members of both species had lower angles (i.e., more pronounced ridges) compared to all other groups (*p* < 0.001, see Table 3). Similarly, the DMR angles of subadult *Pan* and *Gorilla* did not differ from one another nor did those between *Pongo*, *Hylobates*, and *Papio*. *Hylobates*, whose specimens displayed relatively large angles, was the only group that differed from the subadult *Gorilla* and subadult *Pan* (Table 3).

Relative DMR height also varied among genera (Kruskal-Wallis *H* = 32.725, *p* < 0.001, Figure 5b). Pairwise posthoc tests indicated that adult *Gorilla* differed from all other genera with the exception of

adult *Pan* (Table 3). The DMR heights of adult *Pan*, subadult *Pan*, and subadult *Gorilla* did not differ from one another. The DMR heights of *Papio* specimens were significantly lower than those of adult and subadult *Pan* members but were not statistically different from the heights observed in subadult *Gorilla* (Table 3).

3.2.3 | Dorsal metacarpal ridge comparisons between sexes

The DMR angles of males and females did not differ in *Pan* or *Gorilla* (*Pan*: Mann–Whitney $U z = -1.217$, $p = 0.240$, $n = 20$ females and 7 males; *Gorilla*: Mann–Whitney $U z = -1.20$, $p = 0.244$, $n = 11$ females and 17 males). There was also no difference between the sexes with regard to DMR height in either genus (*Pan*: Mann–Whitney $U z = -0.885$, $p = 0.400$; *Gorilla*: Mann–Whitney $U z = -1.341$, $p = 0.191$). There were an insufficient number of *Papio* specimens for sex comparison analysis; however, ridges were present in approximately 60% of the male and female specimens whose sex was known (3/5 and 7/12, respectively).

4 | DISCUSSION

Documenting ontogenetic transitions in knuckle-walking requires taking two variables into consideration: 1) the amount of time individuals engage in terrestrial and arboreal quadrupedalism and 2) the breakdown of hand postures within those types of quadrupedalism. Sarringhaus et al. (2014) and Doran (1992) found that as chimpanzees aged, the amount of time they spent moving quadrupedally increased. However, neither study documented the ontogeny of hand usage with regard to substrate usage. This study analyzed arboreal and terrestrial quadrupedalism separately. We found that terrestrial quadrupedalism increased with increasing age, with significant increases in the transitions from old infancy to juvenility and from juvenility to adolescence. While moving quadrupedally on the ground, chimpanzees of all ages did so only using knuckle hand postures. In terms of frequency, arboreal quadrupedalism did not vary between age groups.

However, chimpanzee hand postures did vary across development during arboreal quadrupedal locomotion, with knuckle-usage increasing with increasing age. Young infants, old infants, and juveniles primarily used palmigrade postures during arboreal quadrupedalism, while adolescents and adult chimpanzees typically knuckle-walked while arboreal. Notably, infants engaged in knuckle-walking only a small part of the time. The most pronounced shifts involving increased knuckle-usage took place at juvenility and at adolescence.

After clarifying how wild chimpanzees use their hands during locomotion and how both quadrupedal frequency and quadrupedal hand usage change with age, we proceeded to investigate the relationship between knuckle-walking and the prevalence and prominence of the DMR. We measured the DMR angle in addition to height to examine the sharpness of the incline of the ridge. Relatively larger ridges potentially provide greater resistance against dislocation of the proximal end of the phalanx during hyperextension at the metacarpophalangeal joint. We partitioned the subadult group into four different age categories and found significant differences among groups of subadults. The DMR ridge is completely absent in young infants, and does not emerge until older infancy (M1 dental stage) in chimpanzees. It then reaches adult prominence in terms of DMR height during juvenility (M2 dental stage) when individuals begin to knuckle-walk frequently. A difference in relative height appears only between infants and adults. The mean DMR angle, however, does continue to increase after juvenility.

If knuckle-walking generates ridge formation (a component of hypotheses 1 and 2), the feature should *not* appear before the behavior is introduced into the locomotor repertoire, but instead after some delay. This is what occurs in chimpanzees, namely, there is some knuckle-walking during the young infant stage that precedes ridge development. The DMR does not appear until old infancy (between M1 and M2 emergence), *after* the onset of knuckle-walking. This

finding fails to support a central tenet of the null hypothesis (H0), that the DMR is not at all behaviorally induced and will fail to track the onset of knuckle-walking in chimpanzees.

Although the prominence of the DMR angle continues to increase steadily over the course of development, the adult relative ridge height is established in juvenility when individuals begin to knuckle-walk as the predominant mode of locomotion. While the relationship between strain components and cortical bone modeling/remodeling is complex and poorly understood (Huiskes & van Reitbergen, 2005; Judex & Rubin, 2010), cortical bone plasticity, when present, does not typically display a linear relationship with loading frequency. Instead it responds to a minimal number of strains, after which increased loading cycles produce no additional bony response until the event of fracture (Rubin & Lanyon, 1984; Rubin & Lanyon, 1985; Umemura et al., 1997). We are unaware of similar experiments investigating bone modeling/remodeling in the metaphyseal regions of the long bone shaft, and it is possible that distal metacarpal bone ridge formation may be dissimilar to patterns of appositional bone growth shown in prior studies. Articular surface shape and size have been shown to remain relatively constant over development, and are not strongly influenced by behavior (Lieberman, Devlin, & Pearson, 2001; Ruff & Runestead, 1992; but see Plochocki, 2004). Pathological ridge formation has been documented on the dorsal surface of the distal hallux in humans (Bingold & Collins, 1950; Chou, 2000), but the pathological remodeling seen in such examples of osteoarthritis (Martel-Pelletier et al., 1998; Mueller & Tuan, 2011) is likely not applicable to the modeling/remodeling that occurs in nonpathological dorsal metacarpal ridge formation in nonhuman primates. Regardless of the process of bone adaptation, our findings leave open the possibility that infant levels of terrestrial knuckle-walking may induce ridge formation on the dorsal MC.

Subadult *Gorilla* followed a similar pattern to subadult *Pan* in terms of DMR emergence with no individuals displaying ridge
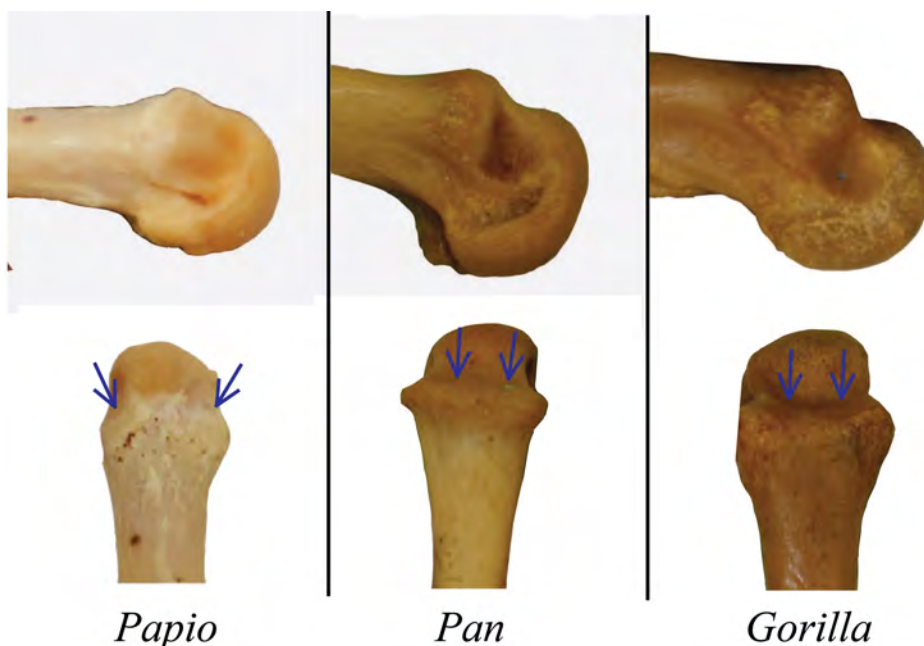

FIGURE 6 The DMR of *Papio*, *Pan*, and *Gorilla* in medial (top) and dorsal (bottom) view. When present in *Papio*, the DMR is two separate ridges angled to the lateral and medial side (blue arrows). The DMR of African apes (*Pan* and *Gorilla*) presents as a continuous ridge from the medial to lateral edge of the distal dorsal metacarpal (blue arrows)

formation before M1 development and most individuals displaying ridges by M2 development. Our *Gorilla* sample is composed of *Gorilla gorilla* and *Gorilla beringei*, as the sample was small, and we elected to make comparisons at the level of genus. Adult *Gorilla* of both species are understood to be less arboreal compared to *Pan* (Doran, 1997; Doran & Hunt, 1994; Remis, 1998), but studies of locomotor development exist for only one population of gorillas, Virunga mountain gorillas (*Gorilla beringei beringei*; Doran, 1997). That study found that knuckle-walking predominates in the Virunga gorilla behavioral repertoire by one year of age (Doran, 1997), much earlier than in *Pan*, for whom knuckle-walking gradually develops and does not become the predominant locomotor mode until juvenility. Given that no infant gorillas (i.e., no M1 present) measured in our study had a DMR ($N = 5$) but about half of those at the later development stage (M1 emerged, but without M2 emerged) did have an incipient DMR ($N = 8$ of 17 total), it is possible that gorilla DMR development lags further behind their locomotor development, and is distinct from *Pan*. It is worth noting that while many developmental and life history milestones have been found to overlap between *Gorilla* and *Pan* (Robbins & Robbins, 2021; Smith et al., 1994; Stoinski et al., 2013), Virunga mountain gorillas may have faster life history trajectories and development compared to other gorillas, and even other populations of mountain gorillas (e.g., see body size discussion in Galbany et al., 2017; weaning in Robbins & Robbins, 2021; skeletal maturation in Taylor, 1997; but also see Kralick et al., 2017 for a review of dental development). Additional study of locomotor development in lowland and mountain gorillas, and a larger subadult morphological sample that is specific to different populations of *Gorilla* will be needed to clarify the factors contributing to these patterns of DMR emergence in *Gorilla*.

Previous research has suggested that because the ridge is not always found on the third MC of all individuals, it is not necessary for knuckle-walking performance (i.e., it is not a critical stabilizer at the MCP joint) but rather a plastic bony response to hyperextension at the MCP joint (Inouye & Shea, 2004). Our data indicate this feature was present in most (97%–98%) but not *all* African ape individuals, as shown by Inouye and Shea (2004). Furthermore, we provide evidence of within-genus variability with a slight ridge occurring in a few *Pongo* specimens ($N = 3$). However, the level of ridge height in these *Pongo* specimens is lower in relative and absolute terms compared to *Pan* old infants (Table 2 & Figures 4b and 5b). Both types of rare occurrences (absence in African apes, presence in *Pongo*) appear independent of body size. Our finding that there are no sex differences present in DMR angle and height in sexually dimorphic *Gorilla* also supports the contention that this feature is not tightly driven by differences in body size. In addition, Inouye and Shea (2004) found that the presence or absence of the DMR did not correlate with body size in chimpanzees and gorillas.

Variability in locomotor performance is understudied in wild ape populations. For example, no information is currently available regarding inter-individual variability in the degree of hyperextension at the MC joint in great apes as they move on different substrates in the wild. However, there are some indications of variable hand usage in

Gorilla and *Pongo*. Thompson et al. (2017) found that knuckle is the most common but not the only hand posture used during terrestrial quadrupedalism in mountain gorillas; several individuals displayed other hand postures frequently, including fist walking with metacarpal heads in direct contact with the substrate. This variation does not occur in chimpanzees as shown here. Nevertheless, there may be variation among chimpanzees (and other apes) in the digit that bears the most weight. It is also important to note that while *Pongo* are primarily arboreal (Manduell et al., 2012; Thorpe & Crompton, 2006), it is not uncharacteristic for them to be terrestrial in the wild (Mitani, pers. obs., Ancrenaz et al., 2014; Ashbury et al., 2015; Loken et al., 2013), and observations in captivity have documented individuals utilizing different terrestrial hand postures, including knuckle-walking (Susman, 1974; Tuttle, 1967). Such data suggest that variation in morphology does not preclude a behavioral influence on the formation of the DMR in great apes.

Despite the occasional absence of the DMR in knuckle-walking chimpanzees, our findings indicate the DMR is more prevalent and prominent in knuckle-walkers (*Gorilla* and *Pan)* than in suspensory taxa (*Pongo* and *Hylobates*). This is consistent with the hypothesis (H1) that the DMR reflects knuckle-walking. The results presented here also provide partial support for the hypothesis (H2) that the DMR reflects terrestrial vertical manus terrestrial postures with hyperextended MCP joints (including both knuckle-walking and digitigrady). Our analysis revealed that about a half of the baboons sampled in this study display a DMR. These animals move quadrupedally using their digits and occasionally their palms to contact the substrate (Napier & Napier, 1967; Patel, 2010; Patel & Wunderlich, 2010; Zeininger et al., 2017). Further examination of *Papio* DMR formation in baboons during development and in relation to ontogenetic changes in locomotion (as performed in this study for *Pan*), will be needed to determine why ridges fail to appear about half the time in this species. The predictions of the null hypothesis (H0), that the DMR will fail to track knuckle-walking and does not vary among genera according to hand usage, were not upheld by our findings.

While the DMR appears in knuckle-walking and digitigrade individuals, it is possible to distinguish the two, as the DMR in African ape knuckle-walkers is more prominent than that in digitigrade *Papio*. The former display more acute angles and larger relative heights (LN height/MC diameter) than do the latter. This observation leads us to provisionally suggest that a ridge can be diagnostic of knuckle-walking if it exceeds a threshold ratio of 0.13 (DMR height/MC midshaft AP diameter; Figures 4 and 5). We also found a qualitative difference in ridge morphology between knuckle-walking African apes and digitigrade *Papio*. The DMR in *Pan* and *Gorilla* spans the dorsal surface of the third MC, while the *Papio* DMR is typically composed of two ridges, one angled medially and one laterally, that do not connect on the dorsal midline (see Figure 6). These preliminary qualitative observations call for further examination of the dorsal MC morphology of habitually terrestrial digitigrade primates.

In sum, results of this study provide the first quantitative analysis of hand contact and substrate use during quadrupedal locomotion in

wild chimpanzees of different ages. These data are required to understand the biomechanical signals experienced by the hands and wrists of these animals. Increases in chimpanzee knuckle-walking mirror increases in quadrupedal locomotion during different periods of development. Changes in the DMR angle and height correspond to developmentally mediated shifts in the frequency of knuckle-walking behavior. The DMR appears to be a terrestrial quadrupedal walking feature that is most prevalent and prominent in adult chimpanzees and gorillas. It is less prevalent and prominent in baboons. By contrast, it occurs rarely and is not very prominent in orangutans, and it is entirely absent in gibbons. Provisionally, we propose this feature is diagnostic of knuckle-walking when it exceeds a DMR height/MC diameter threshold of ~0.13 (see Figure 5). Because the timing of the development of the DMR occurs after the initial transition to knuckle-walking, the loads produced by knuckle-walking likely influence the development of this trait. This study does not resolve whether the DMR is a functionally salient trait that acts as a buttress to prevent hyperextension rather than a byproduct of knuckle-walking that reflects dorsal loading but does not contribute to joint stability. To date, only a handful of epigenetic features have been identified and used to reconstruct the locomotor behavior of fossil hominoids (Ward, 2002). These include the femoral bicondylar angle (e.g., Tardieu, 1999; Tardieu & Trinkaus, 1994) and lumbar lordosis (e.g., Nakatsukasa, 2004; Nakatsukasa & Hayama, 1996). Results from this study furnish provisional support for one additional plastic feature indicative of a particular locomotor mode during the course of ontogeny, namely that the DMR reflects a vertical manus terrestrial quadrupedal posture. However, the quantitatively lower expression and qualitative differences in appearance between the DMR in adult African apes and *Papio* augur well for being able to differentiate between a DMR that reflects knuckle-walking versus digitigrady in a fossil taxon. Pending the discovery of relevant hominoid fossils, the results of such analyses could help resolve whether a terrestrial quadrupedal phase preceded human bipedal evolution.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Lauren Sarringhaus: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **John C. Mitani:** Conceptualization (supporting); funding acquisition (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Laura M. MacLatchy:** Conceptualization (supporting); funding acquisition (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (supporting).

DATA AVAILABILITY STATEMENT

Data that supports the findings are available upon request from authors.

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ENDNOTE

[1] These references do not explicitly examine bony ridge formation near the epiphyseal plate, which may utilize different developmental pathways.

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